

OPINION

Taxonomic aggregation does not alleviate the lack of consistency in analysing diversity in long-term phytoplankton monitoring data: a rejoinder to Pomati *et al.* (2015)

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SUMMARY

1. Long-term phytoplankton monitoring provides an important resource for studying the effects of environmental change on communities and testing ecological hypotheses. However, because of identification difficulties, maintaining consistency in the data over long periods is extremely difficult. It is usually assumed that consistency is improved when only one taxonomist is responsible throughout, and/or when data are aggregated to a coarser taxonomic level. Neither assumption has been critically tested. We address the comment of Pomati *et al.* (2015) on our earlier Opinion paper (Straile *et al.*, 2013) and test these assumptions with the long-term data from Lake Zurich.

2. We show that aggregation to coarser taxonomic levels does not improve data set consistency because: (i) the proportional effect of misclassification is unlikely to be reduced by lumping taxa since the fewer misclassifications affect the dynamics of an overall lower number of taxa, that is the proportional effect is constant, and (ii) because changes in detection limits will affect all taxonomic levels proportionally.

3. We also show that, although a single taxonomist supervised phytoplankton recordings, data consistency is undermined by: (i) learning via exchange with other taxonomists and participation in taxonomic workshops, and (ii) a reduction in detection limits of species, presumably due to an increase in the number of taxonomists (allowing an increased processing time per sample).

4. As a consequence of (i) a reduction in detection limits, (ii) the confirmed taxonomic learning and (iii) the failure of taxonomic aggregation to improve consistency, our new evidence strengthens the view that there are consistency problems in the Lake Zurich data set, and the need for a critical review of the conclusions of Pomati *et al.* (2012) and Matthews & Pomati (2012).

Keywords: data set consistency, phytoplankton monitoring, taxonomic aggregation, taxonomic learning

Introduction

In an earlier Opinion paper (Straile, Jochimsen & Kümmerlin, 2013), we used data from two neighbouring lakes, Lakes Zurich and Walen, sampled by the Wasserversorgung Zurich (WVZ) to highlight general problems of consistency in long-term monitoring data for studies of planktonic diversity. Pomati and col-

leagues used Lake Zurich data from the time period 1977 to 2008 to study long-term development of phytoplankton species richness (Pomati *et al.*, 2012) and the relationship between richness and species-turnover (Matthews & Pomati, 2012) but without addressing the consistency problems identified in our study (Straile *et al.*, 2013), which suggested to us that their conclusions should be reconsidered.

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In their comment about our Opinion paper, Pomati *et al.* (2015) 'conclude that the results of Pomati *et al.* (2012) are robust and not substantially undermined by the criticisms of Straile *et al.* (2013)'. They continue by saying that: 'More generally, it is indeed possible to extract meaningful signals of biodiversity change from long-term phytoplankton monitoring data sets, provided there is a clear understanding of how the data have been sampled, recorded and analysed over the history of the time series'.

We appreciate the opportunity to respond to the comment by Pomati *et al.* (2015) and show here that their previous results are indeed insufficiently robust to support this view and that their latter conclusion is not warranted. Indeed, a clear understanding of phytoplankton monitoring data is an important and necessary condition for extracting meaningful (i.e. accurate) signs of biodiversity change. However, clear understanding is not a sufficient condition for extracting meaningful signals, as it might result in the recognition that a given hypothesis cannot be tested with the monitoring data at hand. In their comment on our Opinion paper, Pomati *et al.* (2015) revised their view on how the phytoplankton data of Lake Zurich were sampled, recorded and analysed, which resulted in a refined species list and a considerable reduction in the estimate of phytoplankton richness in recent years [i.e. a maximum species richness of ~120 in Pomati *et al.* (2012; their Fig. 3) was reduced to a maximum species richness of ~100 in Pomati *et al.* (2015, Fig. 3d)]. We thank Francesco Pomati *et al.* for providing us with this filtered data set. All analyses of Lake Zurich phytoplankton presented here are performed with this refined data set.

The robustness of the conclusions of Pomati *et al.* (2012) and Matthews & Pomati (2012) depends critically on: (i) the absence of a stepwise shift in richness due to a reduction in detection limit and (ii) the consistency of taxonomic identification throughout the study period. Here, we address these two topics, taking this opportunity to discuss two assumptions often made by ecologists (including Pomati *et al.*, 2012, 2015) who are analysing changes in phytoplankton richness: (i) that involving the same personnel throughout ensures data consistency over long periods and (ii) that aggregating taxa to coarser levels results in increased robustness of biodiversity patterns.

Was there a stepwise shift in richness attributable to changes in detection limit?

We acknowledge that Pomati *et al.* (2015) identified the problem with consistency in the data arising from a

change in how the concentrations of cells were entered into the database, and that this methodological change did not cause the drop in the detection limit in the mid-1990s. However, the abrupt increase in taxon richness in Lake Zurich (and Walen) is still unexplained. Indeed, Pomati *et al.* (2015) suggest that 'potential changes in methodology, such as changes in detection limits, should result in stepwise changes in richness pattern'. Surprisingly, they go on to state that such stepwise changes 'are not evident for trends in phytoplankton families and orders (Fig. 3d)'. On the contrary, however, a stepwise increase is clearly visible in their Fig. 3d at all taxonomic levels. Although already evident in their Fig. 3d, the stepwise increase in richness is masked to some extent by the seasonality of richness dynamics and taxonomic learning (see below).

To check for the presence of a stepwise richness increase at the species and order level, we removed seasonality from both time series and tested for a breakpoint using the OLS CUSUM test implemented in the R package *strucchange* (Zeileis *et al.*, 2003). Analyses revealed three breakpoints, both for species and for orders (Fig. 1a, c): A major breakpoint in 1996 (March 1996 for species and in May 1996 at the order level) with 95% confidence intervals from January 1996 to June 1996 for species, and April 1996 to September 1996 for orders. There were two other breakpoints in 1986 and the early 2000s (June 2002 for species, and July 2004 for orders). The narrow confidence intervals for the 1996 shifts underline the abruptness of the observed changes. The shift in 1996 amounted to 51 and 46% for species and orders, respectively, of the overall increase in richness from the first period (i.e. up to 1986) to the most recent period (from 2002 and 2004, respectively) identified by breakpoint analysis. A fit of the richness data assuming step-wise responses (not shown) is much better than a linear fit for both species and orders (for both taxonomic levels, difference in AIC > 100), strongly suggesting that there was no 'steady accrual in richness over time' (Pomati *et al.*, 2015). Furthermore, the striking step-wise richness change in 1996 is responsible for roughly 50% of the overall increase in richness at both the species and order levels.

The year 1996 was also distinctive in terms of seasonal diversity dynamics (Fig. 1b, d). On average (excluding 1996), species richness increased at a rate of 1.1 ± 0.62 (SD) month⁻¹, while ordinal richness increased by 0.3 ± 0.2 month⁻¹. However, in 1996, species richness increased at a rate of 3.1 month⁻¹ and ordinal richness at 1.1 month⁻¹. That is, at both taxonomic levels, the rate of increase in richness in 1996 was more than three standard deviations larger than the average increase for

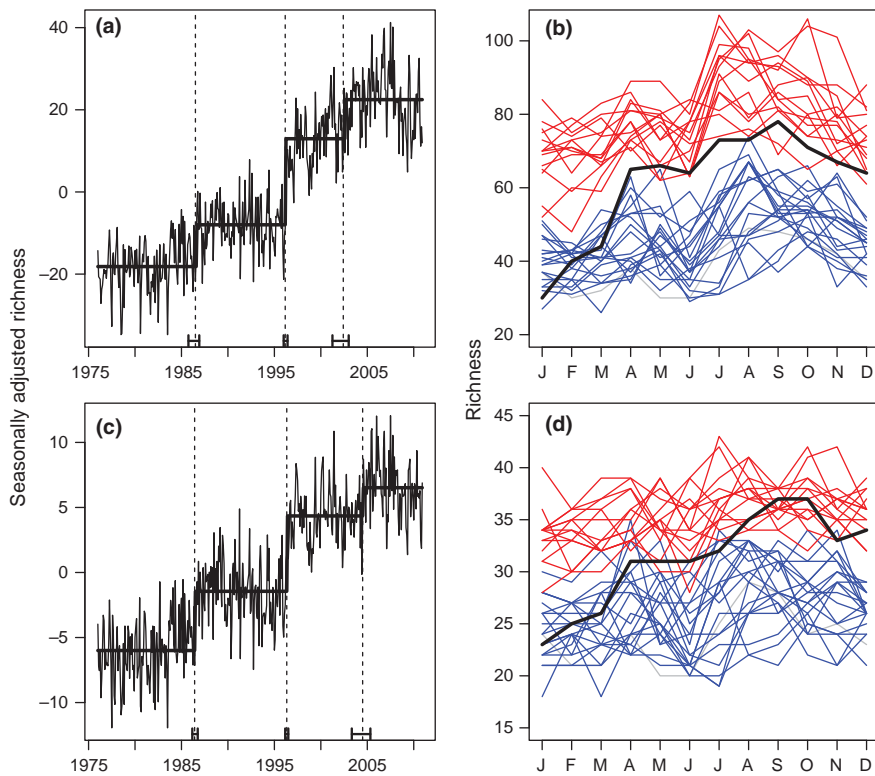


Fig. 1 Seasonally adjusted richness dynamics at the level of (a) species and (c) order, and seasonal richness dynamics at the level of (b) species and (d) order. In (b) and (d), years from 1976 to 1995 are shown in blue, years from 1997 to 2010 are shown in red, while 1996 is shown in black. Breakpoints with 95% confidence limits in (a) and (c) were estimated to have occurred in August 1986 (April 1986–January 1987), March 1996 (January 1996–April 1996) and August 2002 (January 2002–February 2003) at the species level, and in June 1986 (March 1986–October 1986), May 1996 (March 1996–July 1996) and July 2004 (March 2003–May 2005) at the level of order.

any other year, before or after 1996. Hence, an explanation is necessary for why richness after 1996 was so much higher than previously, and why the seasonality of richness dynamics in 1996 differed so markedly from all other years.

As pointed out by Pomati *et al.* (2015), stepwise richness changes may result from changes in detection limits. Following Pomati *et al.* (2015), we used proportional biovolume as an indicator of changes in detection limits. Indeed, the time series of minimum per cent biovolumes of species (orders) provides evidence for a major drop in detection limits that occurred in 1996, both at the species and order levels (Fig. 2). This drop occurred before the WVZ decided to stop rounding up to 1 any values of cell concentrations below that, which occurred in April 1997. The change in data input affected many rare taxa and resulted in a break in the 5% percentile of abundances in April 1997 (Straile *et al.*, 2013), whereas the drop in minimum per cent biovolumes (Fig. 2) is not affected by this change. Rather, this drop occurred 1 year earlier and simultaneously with the strikingly abrupt increase in richness at both the species and order levels. Note that, at the species level, the 1986 minor breakpoint in minimum per cent biovolume also coincided with a stepwise richness increase at the species and order levels. Indeed, and contrary to the statement of Pomati *et al.* (2015: ‘no sys-

tematic change in counting effort over time was noted’), two important ‘methodological’ changes occurred at the WVZ in 1996 (Berger, WVZ, pers. comm).

The first change was that an additional taxonomist was employed in 1996, resulting in less pressure on the taxonomists to analyse the many samples the WVZ had to deal with. As the main objective of the Lake Zurich phytoplankton, time series was to detect changes in biomass, rather than diversity, the identification each cell to species was not a high priority, given that the cell could be grouped into a coarser taxon of similar biovolume. Employment of an additional taxonomist, however, allowed more time for each sample and, hence, more time to identify individual cells. Note that this change will not alter the overall number of cells counted, but has probably resulted in the detection of more rare species at lower concentrations. It is also important to recognise that the new employee in 1996 was an experienced phytoplankton taxonomist bringing new, potentially complementary, taxonomic knowledge. The second change was in the policy for recording new taxa. Before 1996, taxa were recorded in the data base only after they appeared in the lake somewhat regularly (Pomati *et al.*, 2015), whereas after 1996, a taxon was recorded on its very first appearance or upon first identification (Berger, WVZ, pers. comm).

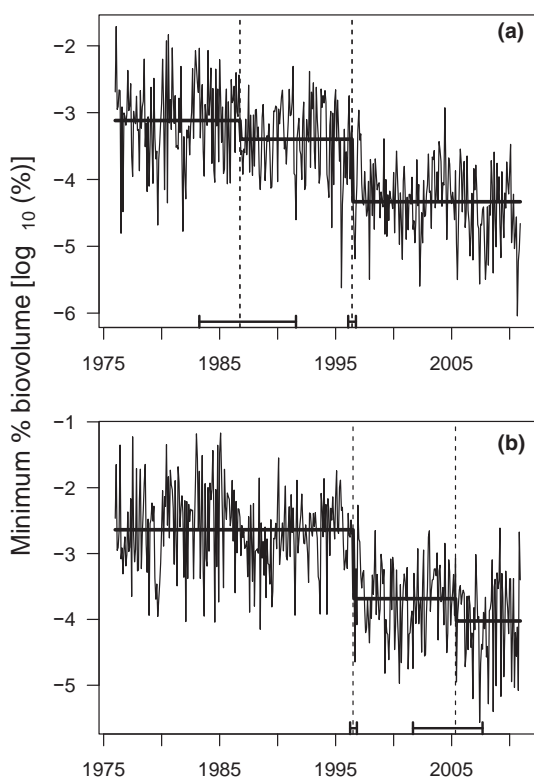


Fig. 2 Minimum percent biovolume for (a) species and (b) orders. Breakpoints with 95% confidence limits were estimated to occur in October 1986 (April 1983–August 1991) and June 1996 (February 1996–October 1996) at the species level, and in July 1996 (April 1996–November 1996) and May 2005 (September 2001–September 2007) at the level of order.

The exact consequences of these changes in methodology on phytoplankton richness are difficult to estimate, although taxonomists at the WVZ confirm that time limitations were important in determining whether particularly rare and difficult taxa were identified to species or genus or aggregated to order or class. In combination, these changes make up a plausible explanation for the abrupt richness increase in 1996 (Berger, WVZ, pers. comm).

In contrast, Pomati *et al.* (2015) suggest environmental change during the mid-1990s drove an increase in richness (Pomati *et al.*, 2012) and a reversal in the relationship between species richness and turnover (Matthews & Pomati, 2012). There are, however, several factors suggesting that environmental change is an unlikely explanation for these patterns.

First, the striking increase in richness in Lake Zurich in 1996 occurred simultaneously with that in Lake Walen (Straile *et al.*, 2013). Both lakes were sampled by the WVZ, with the same methodological changes in processing phytoplankton, but the lakes differ in their

trophic status and phytoplankton composition (Anneville *et al.*, 2004; Anneville, Gammeter & Straile, 2005). Based on the differences in the ecology and trophic status of the lakes, it is difficult to see why such marked shifts should occur simultaneously.

Second, one might expect that such a striking increase in richness would be accompanied by a significant change in the biomass composition of the phytoplankton. However, previous studies of phytoplankton change in these lakes relying on the biovolume of taxa detected no pronounced change in community composition during the mid-1990s (Anneville *et al.*, 2004, 2005).

Third, and contrary to the statement of Pomati *et al.*, [2015: ‘there is clearly a shift in the main environmental descriptors in the mid-1990s... Pomati *et al.* (2012)], no major shift in environmental parameters (e.g. water temperature, water column stability) occurred in the mid-1990s, but an abrupt shift had occurred in Lake Zurich by 1988 (see North *et al.*, 2013, 2014; for detailed analyses of stepwise changes of environmental parameters in Lake Zurich). Clearly there was no response of phytoplankton richness to the water temperature and mixing regime shift in 1988 (Fig. 1). Interestingly, a similar regime shift in water temperature in 1988 was also observed in nearby Lake Constance (Jochimsen, Kümmerlin & Straile, 2013). However, no step-wise increase in richness was observed in 1996 in that lake (data not shown). Of course, ecological responses sometimes do occur with time lags, and we cannot fully exclude the possibility that an 8-year time lag in the richness response could also have occurred in Lake Zurich. However, consideration of the time schedule of the ecological changes in Lake Zurich renders the hypothesis that environmental change was the driver of the 1996 richness shift even more unlikely.

In summary, ~50% of the richness increase in the Lake Zurich phytoplankton occurred within a few months and concurrently with a strong reduction in the minimum cell biovolumes detected by the WVZ taxonomists. The robustness of the results of Pomati *et al.* (2012) and Matthews & Pomati (2012) thus depends mainly on whether the stepwise increase in richness in 1996 was due to methodological changes or to an abrupt real ecological response to a major environmental change some 8 years earlier. Given the evidence above, we suggest that methodological changes are the most likely explanation.

How likely is consistency in taxonomic knowledge throughout long-term phytoplankton monitoring?

The considerable reduction in the number of taxa due to filtering suggests that Pomati *et al.* (2015) acknowledge

that there was substantial taxonomical learning despite the fact that data 'have been acquired by only a very small team of specialists under the supervision of the same person during the entire period' (Pomati *et al.*, 2012). The detailed record of taxonomic changes kept by the WVZ reveals that several taxa first appeared in the data set due to taxonomic learning, either via exchange with other taxonomists or via participation of WVZ taxonomists in taxonomy workshops. For example, a diatom workshop in 2001 resulted in >10 new diatom species, while a chlorophyte workshop in 2004 added one new species (*Coelastrum polychordum*) to the list of taxa. Note that the latter species, in addition to several further species, which new identification is considered by the WVZ taxonomists to be due to taxonomic learning (e.g. *Erkenia subaequiciliata* in 1976, *Chlamydomonas gleophylla* and *Stichococcus sp.* in 1996), are still included in the refined data set of Pomati *et al.* (2015). Hence, the records of the WVZ show conclusively that learning has been an important process right up to the present.

In addition to documented evidence for taxonomic learning, there have also probably been further instances that have not been recorded. Straile *et al.* (2013) have used synchrony of species-occurrence (i.e. within ± 2 years) in lakes Zurich and Walen, both studied by

the WVZ, as a diagnostic tool for identifying 'apparent invasions' (i.e. 'invasions' due to improvements in taxonomic skills rather than genuine invasions). Pomati *et al.* (2015) admit that 'perfect synchrony in invasion of a species can reflect a bias in database compilation', but nevertheless argue that it might also represent an 'ecological signal ... that deserves further analysis'. Many of the invasions, which are likely to be apparent (i.e. rather than real invasions) because they occurred synchronously in the two lakes (e.g. *Erkenia subaequiciliata*, *Katablepharis sp.*, *Tetraselmis sp.* (Fig. 3a)) are indeed confirmed by the WVZ to result from taxonomic learning. Hence, we should be extremely careful in providing ecological theories for the synchronous invasion of any taxon in Lakes Zurich and Walen (e.g. Fig. 3b i). Pomati *et al.* (2015) argue that invasions whose timing differs between lakes Zurich and Walen by more than 1 year 'could represent a real signal'. However, 'perfect synchrony' of apparent invasions should not be expected for taxa occurring at low frequency in one or both lakes. For example, *Merismopedia sp.*, *Closterium acutum* and *Botryococcus sp.* (Fig. 3d f) were identified in Lake Zurich frequently after their first appearance, whereas they were found much less frequently in Lake Walen. The 'invasions' of all three taxa differ in timing between

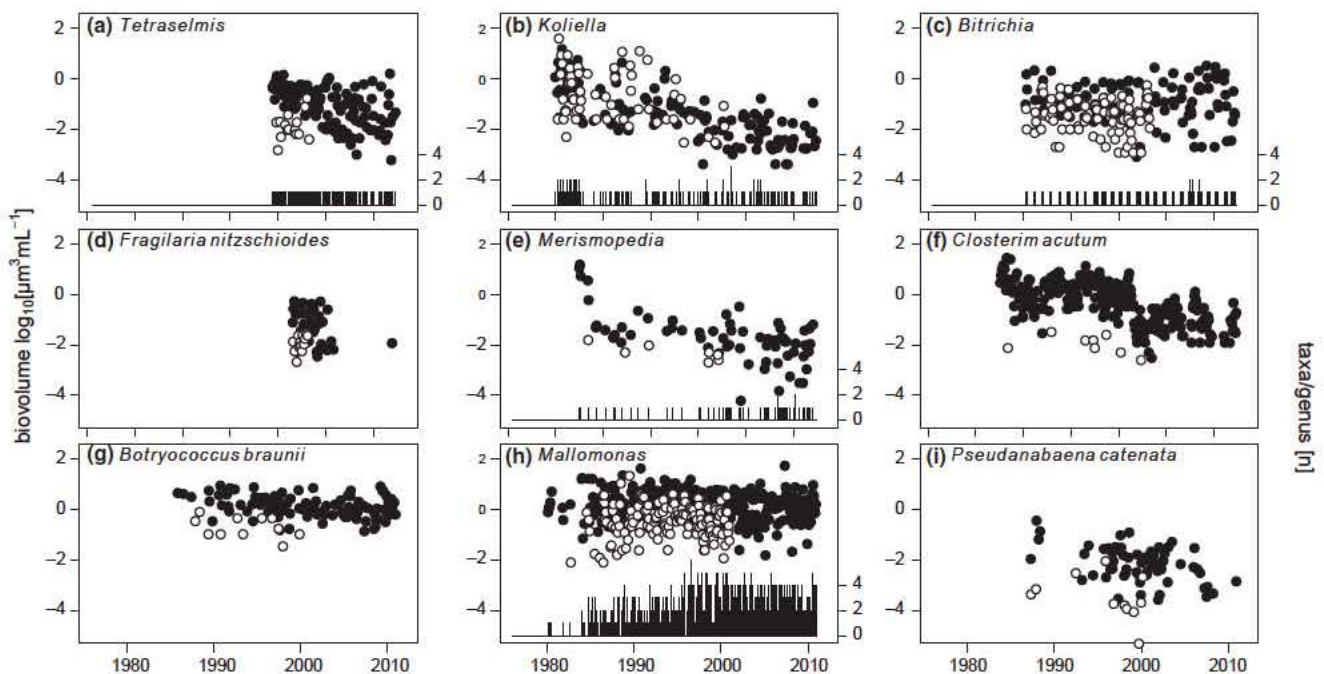


Fig. 3 Time series of taxa in Lakes Zurich (black dots) and Walen (white dots) illustrating dynamics resulting from a confirmed or assumed increase in knowledge: (a) *Tetraselmis sp.*, (b) *Koliella spp.*, (c) *Bitrichia spp.*, (d) *Fragilaria nitzschioides*, (e) *Merismopedia spp.*, (f) *Closterium acutum*, (g) *Botryococcus braunii*, (h) *Mallomonas spp.*, and (i) *Pseudoanabaena catenata*. Note that, for Lake Walen, the time series used (Anneville *et al.*, 2004, 2005) extends only to 2001. For genera, which are represented by more than one species, genera biovolume is shown and the number of species within the genera in Lake Zurich is shown at the bottom of each subpanel as rugs.

lakes Zurich and Walen by more than 1 year. However, phytoplankton lists show that, for instance, *Merismopedia* sp., *Closterium acutum* and *Botryococcus braunii* were already present in Lake Zurich in the 1950s, when the lake was eutrophic (Thomas, 1964). Furthermore, a second time series on Lake Walen phytoplankton from 1967 to 1976 (Ambühl & Florin, 1978) had identified *Merismopedia* sp., and also *Mallomonas* spp. and *Pseudanabaena catenata*, for example, as members of the phytoplankton. Despite their presence, these taxa were not identified by the WVZ in Lake Walen before 1980 and appeared synchronously in the record for both lakes during the 1980s (Fig 3h i). We consider it probable that these taxa were also present in Lake Zurich before 1980 but were not recognised by the WVZ, indicating that ‘synchronous’ initial occurrence (even within a time window exceeding 1 year) is a valuable diagnostic tool for identifying apparent invasions.

Learning will bias richness dynamics not only because first appearances in the record are assumed erroneously to be genuine invasions, but also because of unnoticed extinctions in the early phases of the monitoring. Palaeolimnological studies show that some diatom species, for instance, are present only under eutrophic conditions, whereas others occur only when lakes are oligotrophic (e.g. Berthon *et al.*, 2014). We know that some taxa present in Lake Zurich at the start of the time series could not be identified because of limited taxonomic knowledge at the time. Some of these taxa are still in the lake and have contributed to an apparent increase in species richness as taxonomic skills improved. However, others possibly went extinct before they could be recorded. While the first bias may be corrected by filtering out ‘apparent invasions’, correcting for unnoticed extinctions is difficult if not impossible.

Does taxonomic aggregation really increase the robustness of patterns?

According to Pomati *et al.* (2015), the temporal stability of within-group richness (defined as the number of subordinate taxa at a given taxonomic level) indicates the consistency of the data at the family and order levels. Unfortunately, these diagnostic plots are not sensitive to changes in methodology or taxonomic knowledge, because family or order is rarely used as a level of taxonomic resolution by phytoplankton taxonomists. In the Lake Zurich data set, no cell was identified exactly to family, because either the taxonomist could identify the genus or species, or was not sure about the family and assigned it instead to order or class. Over the entire time

series, cells belonging to three different orders were sometimes only identified as such (the orders Centrales, Chromatiales and Euglenales), while cells of four different classes were sometimes only identified that far (Bacillariophyceae, Chrysophyceae, Hormogoniophyceae, Trebouxiophyceae). There is not a single case in which, due to improved taxonomic knowledge, an order was split into two or more families. Furthermore, Pomati *et al.* (2015) have removed these few coarse taxonomical identifications from the taxon list when using the data set for richness studies. Hence, there is no reason to expect that the number of families within orders should be sensitive to improved taxonomy. The diagnostic plots of Pomati *et al.* (2015) are therefore not appropriate for assessing the consistency of the data at higher taxonomic levels.

Pomati *et al.* (2015) suggest that analyses of richness change at coarser taxonomic levels might be more robust than those at finer taxonomical level because: (i) at coarser taxonomical levels, the probability of error is lower, and (ii) because bias due to misclassification is unlikely to propagate proportionally upward in the classification hierarchy. Unfortunately, neither assumption holds (at least for the Lake Zurich data set). As family or order has rarely been used as a taxonomic identification level in Lake Zurich (see above), new orders always appeared in the record because a new species or genus had been identified. Hence, increases in species richness undoubtedly propagate upwards in the classification hierarchy, and improved taxonomical skills with respect to those species will cause a biased increase in species richness, and as well in ordinal richness. In the Lake Zurich data set, 19 new orders have been identified since 1975. From these 19 orders, 11 (58%) should be considered to be definite or probable errors (i.e. apparent rather than real invasions). These ‘invasions’ are in doubt because they are known or assumed to be not real by the WVZ (Chlorodendrales (*Tetraselmis* sp.; Fig. 3a), Katablephariales (*Katablepharis* sp.), Ochromonadales (*Erkenia subaequiciliata*), Prymnesiales (*Chrysochromulina* sp.)), and/or they were already listed in Thomas (1964) and/or Ambühl & Florin (1978) (Synurales (*Mallomonas* spp.; Fig. 3h), Synchococcales (e.g. *Merismopedia* sp.; Fig. 3e), Trebouxiiales (*Botryococcus braunii*; Fig. 3g). Furthermore, two orders appeared synchronously in Lakes Walen and Zurich (Hibberdiales (genus *Bitrichia* in September 1986 in both lakes; Fig. 3c)), Prasiolales (genus *Koliella* in December 1980 in Lake Zurich and 3 months later in Lake Walen; Fig. 3b)), and two orders represent Gamma-Proteobacteria [Methylococcales (*Crenothrix* sp.), Thiotrichales (*Thiospira* sp.)], which are both likely to have been present in

the lake before they first appeared in the data set (in 1999 and 1996, respectively). This list demonstrates that the assumption that the probability of learning and/or classification error is lower at coarser taxonomic level is not justified for the Lake Zurich data set.

Furthermore, because there are more taxa at a finer than at a coarser taxonomic level, even a small number of misclassifications at a coarser taxonomic level can have a large effect on richness dynamics at this level. For example, the taxon list for Lake Zurich consists of 46 orders, 71 families, 126 genera and 187 species (Pomati *et al.*, 2015). An apparent 'invasion' of one new species representing a new order will increase the number of species by 0.5%, the number of genera by 0.8%, the number of families by 1.4% and the number of orders by 2.2%. Thus, in the case of Lake Zurich, errors will have a larger effect on richness dynamics at the ordinal level than at the species level, unless misidentification of species (from orders already in the record) is four times greater than that of species from new orders. Hence, the proportionate error will depend on the number of new species within orders already represented in the record relative to new species within new orders. This suggests that it cannot simply be assumed that consistency will be greater at coarser taxonomic levels, but there must be critical scrutiny of each phytoplankton time series. With respect to the Lake Zurich data, aggregation to higher taxonomic levels does not result in more robust results: the number of orders present at a specific sampling date is as much as the number of species affected by changes in detection level (Figs 1 & 2), and by improved taxonomic skills.

To conclude, scrutiny of the Lake Zurich phytoplankton record suggests that richness calculations based on this data set are indeed biased. We acknowledge that Pomati *et al.* (2015) also accept this, and they consider that the dynamics of richness is reliable only at family and order levels (see their Fig. 3d). Nevertheless, Pomati *et al.* (2015) used these data to perform secondary analyses at the level of genus (their Figs. 2a,b). It is not clear how any secondary analyses, performed with data evaluated *a priori* as unreliable, can provide evidence for their reliability, even when the results of these analyses appear to be meaningful. Furthermore, the results presented in their Fig. 2a (i.e. the apparent temporal increase in the annual prevalence of rare taxa, despite declining abundances) nicely demonstrate the consequences of reduced detection limits (that is, the chances of detection went up) after 1996. The latter will increase annual prevalence, but will not affect the decline in abundances with oligotrophication.

We want to emphasise that the monitoring data of the WVZ, where monitoring procedures conform to the highest standards, represent an important resource for future ecological research. However, it needs to be recognised that these time series were not initiated to monitor biodiversity, but the biovolume of dominant taxa and total biovolume. It is the responsibility of researchers using these data to understand their limitations, particularly when testing various ecological hypotheses.

Our analyses show that, in the case of Lake Zurich, there was a striking step-wise increase in richness amounting to roughly 50% of the overall richness increase. We provide strong evidence that methodological change, rather than ecological change, is a more likely explanation for this increase. Furthermore, because of taxonomic learning, a considerable part, if not all, of the remaining 50% of richness increase in Lake Zurich is also not real. More generally, our analyses suggest that, for phytoplankton time series, it cannot simply be assumed that a) continuous employment of the same taxonomist (although of course a genuine advantage) and b) working at coarser taxonomic level, mean that the data are robust. This needs to be tested for each data set and, for Lake Zurich, these assumptions do not hold, which is a serious problem when testing hypotheses concerning biodiversity. Consequently, the conclusions of Pomati *et al.* (2012) and Matthews & Pomati (2012) may not be robust and need to be reconsidered.

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